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ORIGINAL ARTICLE

Antipredator Behavioral Responses of Native and Exotic Tadpoles to Novel Predator

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Abstract Factors related to the invasion process, such as high abundance of invaders, residence time, and functional distinctiveness, are well documented, but less attention has been given to the effects of antipredator strategy of invasive species during colonization. In this study, we explored the antipredator strategy of an introduced species by comparing the predator avoidance behaviors of two native anuran species and one introduced ("exotic") species in the presence of different predators. The two native anuran species used in the study were Black-spotted Pond Frog *Rana nigromaculata* and Terrestrial Frog *Rana limnocharis*. The introduced (invasive) species used was American bullfrog *Lithobates catesbeianus*. Chinese pond turtle *Chinemys reevesii*, Red-backed rat snake *Elaphe rufodorsata*, and Big-headed turtle *Platysternon megacephalum* were used as predator species. Chinese pond turtles and Red-backed rat snakes are native predators of Black-spotted Pond Frogs and Terrestrial Frogs, while Big-headed turtles are novel ("unfamiliar") to the two frogs. All three predator species are novel ("unfamiliar") to the American bullfrog. The results show that tadpoles of the two native species displayed behaviors of recognizing the two native predators, but did not display the capability of identifying the novel predator. Results from our study also suggest that American bullfrog tadpoles exhibited strong antipredator behavioral responses by displaying the capability of identifying "unfamiliar" predators without cohabitation history and prior exposure to them. Such antipredator behavioral responses could have resulted in more favorable outcomes for an invading species during the invasive introductory process.

Keywords tadpoles, Bullfrog, antipredator responses, chemical cues, novel predator

1. Introduction

Biological invasions threaten biodiversity and lead to species loss and extinction (Ficetola *et al*., 2007). Factors influencing a successful invasion may include: high abundance of invaders, residence time, functional distinctiveness, and disturbance or other changes to the invaded environment (Parker *et al*., 1999; Sax *et al*., 2005; Strayer *et al*., 2006). Understanding the mechanisms of these invasions is currently one of the greatest ecological challenges (Lövei, 1997). In particular, understanding the mechanisms that facilitate the success of an invading species is of considerable importance to the management of the invaders; however, such understanding can be particularly difficult to attain when interactions between native and invading species involve more than a single developmental stage (Kiesecker and Blaustein, 1998). Furthermore, the mechanisms that enable invading species to thrive at the expense of native species are also often unclear (Lodge, 1993).

Although differences in propagule pressure in the first stage are important for a successful invasion (Li *et al*., 2006), we believe that the success of an invasion also depends on the interactions with their own predators and competitors. In other words, successful invasion may be influenced not only by the interactions with native prey, but also by the invader's interactions with new predators, native or not, in the colonized area (Sih *et al*., 2010). According to the "enemy release hypothesis" (ERH), the

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lack or scarcity of an invading species' natural enemy in the introduced environment could contribute to the invading species' establishment and proliferation (Colautti *et al.*, 2004).

For an anuran, one of the primary causes of death for its tadpoles is predation (Alford and Richards, 1999). Many studies have shown that after extensive cohabitation with a predator population, tadpoles of a prey population may develop antipredator behaviors (defenses) such as the capability of recognizing and responding to those predators without any prior exposure (Kats *et al.*, 1988; Kiesecker and Blaustein, 1997; Pearl *et al.*, 2003; Marquis *et al.*, 2004; Sih *et al.*, 2010). These antipredator behaviors could help in the reduction of mortality of the prey tadpole population during the predation process (Marquis *et al.*, 2004; Sih *et al.*, 2010). Sih (1987) classified these anitpredator defenses into two categories: pre-encounter (i.e. the prey tadpoles' ability to recognize predation-related chemical cues released by predators) (Wilson and Lefcort, 1993) and post-encounter (i.e. the release of certain toxic chemicals by the prey tadpoles to reduce their palatability to predators) (Formanowicz and Brodie, 1982). Regardless of which antipredator defense is used, the ability of the invading anuran's tadpoles to recognize non-native predator is vital to a successful invasion. These effective antipredator behaviors could reduce direct predation, thereby resulting in more individuals to attend the establishment stage (Lodge, 1993).

Although antipredator behaviors are important to an invading species during colonization, few studies have been conducted to evaluate the effects of these behaviors**.** Identifying and understanding antipredator strategies of a particular invading species may be crucial to the prevention of future biological invasions process by other alien species. We could focus our effort on interfering with or impairing the antipredator responses of the invading species. This effort may increase the likelihood of predation of the invading species tadpoles, thereby achieving effective control of the invasion.

The American bullfrog, *Lithobates catesbeianus* (also known as *Rana catesbeiana*) is native to eastern North America, but has been introduced in over forty countries and four continents over the last century (Lever, 2003). This species is listed in the Global Invasive Species Database as one of the "100 of the World's Worst Invasive Alien Species" (ISSG, 2008). Bullfrogs can affect native amphibian populations through predation and competition for food and habitat (Kats and Ferrer, 2003; Pearl *et al.*, 2004). Adult bullfrogs act as generalist predators and often prey on other amphibians (Blaustein and Kiesecker, 2002; Kats and Ferrer, 2003). In addition, large bullfrog tadpoles often outcompete the anuran larvae of native species (Ficetola *et al.*, 2007). Consequently, through the combined impacts made by tadpoles and adults, this naturalized bullfrog species has caused population decline or local extinction of native amphibians in some places (ISSG, 2002; Kats and Ferrer, 2003; Ficetola *et al.*, 2007).

American bullfrogs were initially introduced in China during the late 1950s and early 1960s for food trade and commercial farming. (Liu *et al.*, 2010). Based on the information collected from local bullfrog farmers in Nanling County, Anhui Province and the local Committee of Agriculture, we were able to determine that bullfrogs have been established in Nanling County for approximately 25 years. Currently, in many parts of China, the invasions of bullfrogs not only resulted in the decrease in the distribution of native species, but have also resulted in the decline of local frogs populations, to the extent of some local extinctions. (Wu and Li, 2004). We expected the success of this particular invasive species may have been attributed to the capability of its tadpoles having more sensitive and effective antipredator responses to novel predators than other native prey species.

In our study, we sought to compare predator avoidance behaviors of two native tadpole anurans and one introduced tadpole anuran when exposing them to chemical cues from different predator species, novel or native. We suspected bullfrog tadpoles would reduce their activity level more in response to chemical cues from novel predators than that of native tadpole anurans. We also suspected that bullfrog tadpoles would response more vigorously to chemical cues from novel predators who find them palatable than those predators who find them unpalatable. Since reducing actively levels will protect tadpoles from being captured by predators (Kats and Dill, 1998), having sensitive and effective antipredator responses to novel predators will mean more individuals to attend the establishment stage.

The two native anuran species we used were Black-spotted Pond Frog *R. nigromaculata* and Terrestrial Frog *R. limnocharis*. The introduced (invasive) species used was the American bullfrog *Lithobates catesbeianus*. Chinese pond turtle *Chinemys reevesii*, Red-backed rat snake *Elaphe rufodorsata*, and Big-headed turtle *Platysternon megacephalum* were used as predator species. The populations of Black-spotted Pond Frog and Terrestrial Frog coexist extensively in the wild with the populations of both the Chinese pond turtle and the Red-

backed rat snake species (Chen, 1991). In other words, Chinese pond turtles and Red-backed rat snakes are native predators of the two native anurans. The population of Big-headed turtle has never coexisted with the two native anurans in the wild, thus making the predator novel ("unfamiliar") to the pond frogs and terrestrial frogs. Tadpoles of the invasive species came from a commercial bullfrog farm, where the bullfrog population has had no exposure to or interaction with Chinese pond turtles, Red-backed rat snakes or Big-headed turtles, thus making all three predator species novel ("unfamiliar") to the bullfrogs.

2. Materials and Methods

2.1 Animal collection and maintenance During April 2010, we collected tadpoles of three anuran species by hand net. Tadpoles of the two native species, Black-Spotted Pond Frog and Terrestrial Frog, were collected in several small ephemeral ponds and paddy fields in Wuhu County, Anhui Province, China, where native or novel predators were absent. Chinese pond turtles and Red-backed rat snakes are common in these types of ephemeral ponds and paddy fields, but mountain stream turtles, Big-headed turtle, do not inhabit them. Tadpoles of the invasive species, American bullfrog, were collected from a commercial bullfrog farm in Nanling County, Anhui Province, China. These tadpoles were reared from eggs in a commercial bullfrog farm, where Chinese pond turtles, Red-backed rat snakes, and Big-headed turtles did not inhabit.

Tadpoles of all three anurans were transported in separate plastic containers to a laboratory in Anhui Normal University and housed individually in vitreous aquariums (18 cm × 25 cm and 10 cm high) with water at an ambient temperature of about 25 ºC, and under a natural photoperiod (13h:11h light:dark). The tadpoles were fed every two days with a commercial bullfrog tadpole food. No contact with the scent or visual stimuli was allowed before the tadpoles were tested. The tadpole's developmental stage (Gosner's stage: 28; see Gosner, 1960) was standardized within and among the different species.

We captured freshwater turtles in Jing County that are common predators of the tadpoles (Chen, 1991) and used them as predator scent donors. The two scent donor species, adult female Chinese pond turtles and adult female Big-headed turtles, were captured in Jing County in June 2008 and raised in the lab. The turtles were fed two to four appropriately-sized spiny eel (*Mastacembelus aculeatus*) twice a week during their non-hibernation period. We captured the adult female Red-backed rat snakes, common predators of the tadpoles (Chen, 1991), at the Tiantangzhai National Nature Reserve in Jinzhai County in July 2010. We used them as predator scent donors and fed them two appropriately-sized spiny eel once a week during our trial period. We obtained non-predatory goldfish (*Carassius auratus*) from a commercial dealer to be used as the source of neutral scent. Predators, turtles and snakes, were not fed 18 to 24 h preceding an experiment and were never fed any amphibians.

2.2 Chemical stimuli We placed turtles and snakes in separate aquariums. Each aquarium was filled with 5 L of purified water and left overnight to collect the individual's scent. We extracted and packaged the scented water separately in 10 mL portions and tightly sealed to prevent cross-contamination and frozen until use. The brand of purified water used in our experimental trials was Yeling purified water. The neutral stimulus was prepared by placing goldfish, in groups of two, into 3-litre aquariums with purified water for 3 days. Fish were not fed during this short period to avoid any contamination by food odor. Then, 10 mL of water was drawn from each aquarium, packaged, and frozen until use.

2.3 Experimental procedure In order to determine whether anuran tadpoles assess predation risk from native and novel predators differently, we designed a "blind" experiment (Rohr and Madison, 2001; Gonzalo *et al.*, 2007; Polo-Cavia *et al.*, 2010) to analyze swimming activity levels of tadpoles in water scented with chemical cues from the different predators. We observed 15 individual tadpoles of each anuran species in five different treatments ('control water' versus 'non-predatory fish scent' versus 'Chinese pond turtle' versus 'Big-headed turtle' versus 'Red-backed rat snake') in a random sequence. The tadpoles rested for one day between trials to avoid any influence from the previous trial.

The 'control water' treatment was used as a control group; this is where tadpoles were exposed to a predator-free environment**.** The non-predatory 'goldfish scent' treatment was used to test any possible modifications in activity level of the tadpoles due to the presence of any "strange" or unfamiliar scent in the water.

Tadpoles were tested individually in U-shaped gutters (101 cm × 11.4 cm × 6.4 cm) sealed at both ends (see methods in Polo-Cavia *et al.*, 2010). The internal part of each gutter was quartered with four crossing lines to

create five subdivisions of equal surface. We filled each gutter with 3L of purified water at outside environment temperature (25 ºC). We placed a single tadpole covered with a release cage (made of glass: 21 cm × 7.6 cm and 6.4 cm high) in the middle of the central subdivision of each gutter, and waited 5 minutes for acclimation. Then, we put our test solution (scented iced aliquots) at one end of the gutter (either left or right) by stratified randomization, and waited for an additional 5 minutes for the ice to melt. We began our trials by slowly lifting the release cage. This is called a "blind" experiment because the observer was not aware of which test solution was placed in the gutter. Observations were made through a small opening (approximately 15 cm × 8 cm) in an opaque white plastic curtain to minimize disturbance to the test tadpoles. The instantaneous scan sampling method was used to monitor each tadpole continuously for 30 minutes. We counted the number of times each tadpole went through the crossing lines during the entire 30-minute observation period (Rohr and Madison, 2001; Gonzalo *et al*., 2007; Polo-Cavia *et al*., 2010) and recorded the results in 1-minute scan interval. Each 1-minute scan interval represents the number of times a tadpole went through the crossing lines within that one minute (30 scan intervals per tadpole). Diffusion of chemicals in still water may be a slow process, however, we are confident that within the entire 30-minute observation period, all test tadpoles were exposed to our test solutions (Polo-Cavia *et al.*, 2010).

To assess palatability, each palatability experiment contained one predator and 10 prey tadpoles all at the same stage of development (Gosner 28 stages as those tested) in one separate polyethylene tank (35 cm × 23 cm × 22 cm) that was not used in our earlier experiments (detailed procedures can be seen in Wu *et al*., 2008). We used three individuals per predator species group to minimize the possibility of individual taste preferences and all predators were starved for approximately 48 h prior to the experiment. The experiment was repeated three times for all three anuran species with each predator. Each predator was used only once in a single replicate. After 24 h, we recorded the numbers of tadpoles remaining to determine the rate of consumption. Tadpoles that were dead (bitten by predators) but uneaten were replaced so that each predator had the opportunity to consume an equal number of live tadpoles.

2.4 Statistical analyses Swimming activity levels for each tadpole (represented by the number of lines crossed) were log transformed to ensure normality (Shapiro-Wilk's test) and the difference in activity level of the same individual tadpole across the five treatments with water containing different chemical cues (within-subject factor: 'control water' versus 'non-predatory fish scent' versus 'Chinese pond turtle' versus 'Red-backed rat snake' versus 'Big-headed turtle') was tested using one-way repeated measures analyses of variance (ANOVAs). Additionally, homogeneity of variance (Levene's test) was also tested, and the results showed that the variances were not significantly heterogeneous. Pairwise multiple comparisons were made using Tukey's honestly significant difference tests (Polo-Cavia *et al*., 2010).

3. Results

When the activity levels of the three species of anuran tadpoles were tested, we found significant differences in the activity levels demonstrated by the tadpoles between each predator cue treatments (Figure 1). Bullfrog tadpoles showed significantly lower activity levels in water treated with chemical cues from Chinese pond turtles and Big-headed turtles than in control water ($F_{4,70} = 11.45$; $P < 0.0001$). They did not show significant differences in the overall activity levels between water treated with non-predatory fish scent and Red-backed rat snake scent in comparison to their activity in control water (Table 1).

Tadpoles of Black-spotted Pond Frog and Terrestrial Frog reduced their activity in water with chemical cues from Chinese pond turtles and Red-backed rat snakes. They did not significantly reduced their activity in the water treated with chemical cues from Big-headed turtles (Black-spotted Pond Frog: $F_{4,70} = 8.02$; $P = 0.474$; Terrestrial Frog: $F_{4,70} = 10.02$; $P = 0.191$) and non-predatory fish and control water (Table 1).

In the palatability trials, Chinese pond turtles consumed 93% of American bullfrog tadpoles, 97% of Black-spotted Pond Frog tadpoles, and 90% of Terrestrial Frog tadpoles. The Big-headed turtles consumed 100% of American bullfrog tadpoles, 100% of Black-spotted Pond Frog tadpoles, and 87% of Terrestrial Frog tadpoles. The Red-backed rat snakes consumed 100% of Black-spotted Pond Frog and Terrestrial Frog tadpoles, but none of the American bullfrog tadpoles offered to them.

4. Discussion

In our study, we observed that all three of the tadpole species, native or exotic, did not exhibit any antipredator behavioral responses in water treated with a neutral chemical cue (non-predatory fish). Such observation confirmed our belief that antipredator responses in amphibian tadpoles are mediated by water-borne chemical

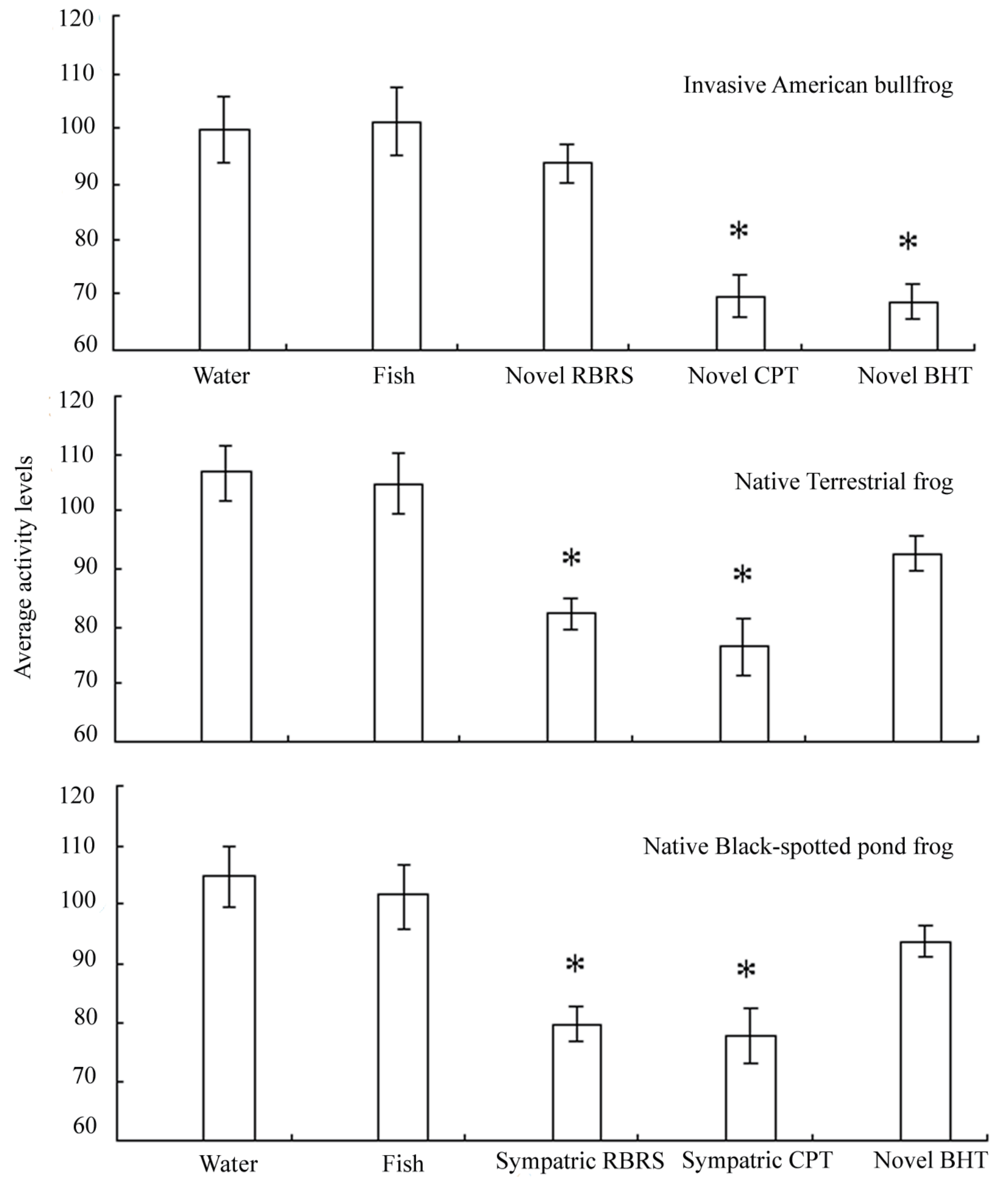

Figure 1 Average activity levels (Mean ± SE number of lines crossed during 30 min) of three species of anuran tadpoles: American bullfrog; Black-spotted pond frog; Terrestrial frog, in trials with control water, water with chemical cues from non-predatory fish, water with chemical cues from three different predator species (RBRS=Red-backed rat snake; CPT=Chinese pond turtle; BHT=Big-headed turtle). *: Significance, $P < 0.05$.

cue, and modification in activity levels occurs when tadpoles perceived predatory threats.

Some studies have demonstrated that anurans tadpoles from populations extensively cohabitating with predatory species are able to recognize and respond to these predators without any prior exposure or contact (Kats *et al*., 1988; Kiesecker and Blaustein, 1997). The results showed that two native tadpoles (Black-spotted Pond Frog and Terrestrial Frog) significantly reduced their swimming activities when scent stimuli from the native predators (Chinese pond turtles and Red-backed rat snakes) were present. Since tadpoles of the two native species were collected in ponds and paddy fields where native or novel predators were absent, such reduction in activity levels indicated that two native tadpole species may be capable of "innately" detecting the presence of native predators.

Moreover, in some cases, although the potential prey do not have an innate ability to recognize the predators, they are capable of learning through experience what are and are not considered as predators (e.g. fish: Mathis and Smith, 1993; Hazlett, 2003). Experience could include the exposure to an alarm chemical cue released by an injured conspecific. Several studies have demonstrated

Table 1 Results (*P* values) of the Tukey's tests examining the responses of Black-spotted Pond Frog, Terrestrial Frog, and American Bullfrog tadpoles to the five different treatments

	Control water	Nonpredator Goldfish	RBRS	CPT	BHT
American Bullfrog					
Control water	–	> 0.99	0.955	< 0.0001	< 0.0001
Black-spotted Pond Frog					
Control water	–	0.986	0.007	< 0.0001	0.474
Terrestrial Frog					
Control water	–	0.996	0.003	< 0.0001	0.191

The treatments were control water, water with chemical cues from non-predatory fish, water with chemical cues from three different predator species (RBRS=Red-backed rat snake; CPT=Chinese pond turtle; BHT=Big-headed turtle).

that this type of acquired predator recognition in both fish and tadpoles by pairing alarm cues with the visual or chemical cues of a predator (Fish: e.g. Chivers and Smith, 1994, 1995; Larson and McCormick, 2005; Tadpoles: Mandrillon and Saglio, 2005). Since the populations of Black-spotted Pond Frog and Terrestrial Frog species share the same distribution areas in the wild as the populations of Chinese pond turtle and Red-backed rat snake species, they may have developed antipredator behavioral responses to these two predator species through learning.

Big-headed turtles inhabit cold (12 °C–23 °C) fast-flowing mountain streams with boulders and gravel in the substrate, and rarely have the chance to encounter either Black-spotted Pond frogs or Terrestrial frogs, which inhabit flat area. Accordingly, Big-headed turtles would be considered an unfamiliar species to Black-spotted Pond frogs and Terrestrial frogs (Chen, 1991). The results showed that activity levels of the native tadpole species (Black-spotted Pond Frog and Terrestrial Frog) did not decline when exposed to chemical cues from the novel predator species (Big-headed turtles). Such results suggested that two native tadpole species may not be capable of "innately" recognizing predator species, whom they have not shared a coevolutionary history with in the wild. Moreover, results of some studies have suggested that some amphibians lack the ability to distinguish between ''dangerous'' and ''less threatening'' predators (Hazlett *et al.*, 2000). The lack of such ability could possibly be due to historically low levels of predation, or because the predators of these amphibians possess the ability to break down or mask cues allowing for such discrimination (Wirsing *et al.,* 2005).

In the current study, tadpoles of American bullfrog significantly reduced their swimming activity when exposed to the chemical cues of the Chinese pond turtle and the Big-headed turtle. However, when exposed to the chemical cue of Red-backed rat snakes, the tadpoles of the American bullfrog did not significantly reduce their swimming activity. The bullfrog tadpoles were collected from eggs reared in a commercial bullfrog farm, where none of the predator species inhabit. If all three predator species are novel ("unfamiliar") to American bullfrogs, why did the variation in antipredator behaviors exist when exposed to the two turtle species and the snake species?

The palatability experiment showed that while Chinese pond turtles and Big-headed turtles consumed most of the American bullfrog tadpoles (Chinese pond turtles 93%, and Big-headed turtles 100%), Red-backed rat snakes consumed none of the bullfrog tadpoles offered to them. Studies have shown that the palatability of a tadpole to a specific predator would affect the tadpole's behavioral responses. For example, Kiesecker *et al*. (1996) found that tadpoles of *Bufo boreas* modified their behavior in response to three predators that find them palatable (two insects and one snake), but did not respond to cues of two predators that find them unpalatable (one newt and one fish). Furthermore, other studies have shown that tadpoles of American bullfrog from their native distribution reduced activity more in response to dragonfly larvae than in response to native mud minnows, which find American bullfrog less palatable than dragonfly (Relyea, 2001). The unpalatability of species may account for their lack of response to chemical cues of a sympatric predator (Laurila *et al*., 1997).

In the current study, bullfrog tadpoles significantly reduced their swimming activity when exposed to the chemical cues of the Chinese pond turtle and the Big-headed turtle, who find them palatable. However, bullfrog tadpoles did not significantly reduced their swimming activity when exposed to chemical cues of the Red-backed rat snakes, who find them unpalatable. We suspect the unpalatability of the American bullfrog tadpoles to the predator may have accounted for the lack of antipredator behavioral responses exhibited by the tadpoles when exposed to chemical cues of Red-backed rat snakes. The combination of the reduction in activity level and the results of our palatability experiment suggested that

American bullfrog tadpoles may be capable of “innately” identifying novel (“unfamiliar”) predators without prior co-occurrence and without prior experience (Pearl *et al*., 2003). The variations in activity levels to different novel predators also indicated that bullfrog tadpoles might be capable of identifying more dangerous novel predators who might find them palatable, thereby modifying their behaviors to respond to the threat of predation.

Hazlett (2000) considered that such behavioral modification exhibited by the bullfrog tadpoles in response to more dangerous novel predators could have contributed to their success as an invasive species. The ability of the invasive species tadpoles to discriminate the chemical cues from novel predator might represent a competitive advantage. During colonization, an invading species can sometimes become a prey species in the colonized area due to its lack of a coevolutionary history with native predators. If the antipredator behaviors of the invading species are based on the “familiar” predator theory, then, the invaders will exhibit nonexistent or ineffective antipredator responses, which may lead to an unsuccessful introduction. Invasive species tadpoles may be able to respond to novel predators’ cues because cues from the novel predators may be similar to cues from the tadpoles’ native predators. Accordingly, we suspect there may be similar cues exhibited by the bullfrog’s native predators and the behaviors of our novel predators, the Chinese Pond turtle and Big-headed turtle.

Our results suggested that the three tested anuran tadpoles were able to differentiate between predator cues and may reduce their activity level as a function of both coexistence history and palatability. Faced with the risk of predation, the prey may display various defense mechanisms to avoid or reduce such risk, thereby maximizing their survival rate (Sih, 1980). In the current study, we demonstrated that American bullfrog tadpoles were capable of distinguishing scents from novel predators by exhibiting antipredator behavioral responses. Accordingly, tadpoles of American bullfrog in the wild may also be able to discriminate novel predators without cohabitation history and prior exposure to them. Strong antipredator behavioral responses may result in a favorable outcome in the establishment and prevalence of this invasive species during the colonization process.

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